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THE EFFECT OF TEMPERATURE UPON THE DEVELOPMENT OF THE EYE OF DROSOPHILA

By

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A.B. Franklin & Marshall College 1914

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THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ZOOLOGY IN THE GRADUATE SCHOOL OF THE UNIVERSITY OF ILLINOIS, 1922

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THE GRADUATE SCHOOL

May 12 1922

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Amos Henry Hersh

ENTITLED The effect of temperature upon the development of the eye of Drosophila.

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE DEGREE OF Doctor of Philosophy

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439035

THE EFFECT OF TEMPERATURE UPON THE DEVELOPMENT OF THE EYE OF DROSOPHILA.

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I. Introduction.

Facet number in Drosophila melanogaster Meig is a character which is modified by germinal changes and by environmental (temperature) changes. In the bar series of multiple allelomorphs the bar and ultra-bar genes, each cause a reduction in facet number over the full-eyed condition. Increased temperatures also cause a change in the number of facets in the same direction.

The question arises, "what takes place during development to produce the change in facet number in the adult and furthermore how does the manner of action of the germinal differences agree with the manner of action of the temperature differences?" From the viewpoint of experimental embryology, the question may be stated more specifically, as follows: What is the embryological mechanism which produces a difference in facet number in flies of the same genetic constitution raised at different temperatures? And how does this mechanism compare with that which produces a different facet number in two races of flies of different germinal constitution raised at the same temperature?

Another phase of the problem arises in connection with flies heterozygous for the various genes. Does facet number in such flies show the same temperature relations as facet number in homozygous stocks? And here again what is the embryological mechanism involved in the production of the character in the adult, and how does it compare with the mechanism in homozygous stocks? The present study is a contribution toward the solution of the facet problem as outlined above. It consists of two parts, one

which deals rather with the embryological side of the problem, and the other which takes up the study of the effect of temperature upon the heterozygous condition.

It may be pointed out here that the bar series is material of the first rank for an investigation of this sort which aims to express germinal values in terms of the environment and to seek the manner from an embryological viewpoint by which a gene becomes expressed in the soma. This utility depends upon the facts that germinal and environmental differences cause modifications in facet number in the same direction, that heterozygotes give an intermediate condition, and that the event which in some sense determines the facets of the adult has been determined relative to the period of embryonic development.

This work was carried out in the zoological laboratories of the University of Illinois. The series of temperatures was made possible by the splendid equipment of the Vivarium Building. It is a pleasure to acknowledge my indebtedness to Professor Charles Zeleny under whose direction the work was done, for his valuable and helpful criticisms and suggestions. I also wish to thank Miss Roselle M. Karrer, who has allowed me to use her data on full-eyed Drosophila.

II. Embryology.

Introduction: The object of the work was to raise larvae at different temperatures -- the temperatures chosen were 17° C. and 27° C. -- and by a study of the larvae during the facet reaction period as determined by Krafka (1920), it was hoped to find the explanation from an embryological point of view for the difference in the facet counts of the adults at these temperatures.

A successful completion of the object of this phase of the work necessarily must rest upon a full knowledge of the normal development of the ommatidia of the compound eye. The state of our knowledge of this subject from the viewpoint of a determination of what constitutes the difference on the one hand between flies of the same stock raised at 17° C. and 27° C. and on the other hand of flies of different germinal constitution but of the same facet count at the same temperature leaves much to be desired. There has been no work done to show the condition of the optic discs during the time of facet reaction.

Materials and Methods: A low bar stock was used for this work. This is the same stock which was used in the study of the effect of temperature upon the heterozygous flies.

Culture Methods: The flies were raised upon fermented banana in 8 dram vials at 17° C. and 27° C. By removing the parents from the bottles several hours after their being placed at the experimental temperature, the age of the larvae could be determined within several hours. This does not mean, however, that all larvae of the same age in point of time are necessarily in the

[illegible]

[illegible]

[illegible]

[illegible]

same stage of development.

Technique: Petrunkevitch's modification of Gilson's fluid and Allen's modification of Bouin's fluid, his B15, were used in fixing the larvae. Sections were cut 6 microns in thickness, and all stained with iron haemotoxylin. The study of sections was supplemented by dissection of the larvae under binoculars.

Origin and Development of Optic Discs: The groundwork of our knowledge of the development of the compound eye in the Diptera was laid by the work of Weismann. It is true that some of the earlier workers saw and described the structures in the larvae which we now know give rise to the imago; Swammerdam probably was the first to see them. The earlier workers, however, did not guess correctly as to what they were. It was Weismann who determined their true nature, and named them "Imaginal Scheiben", and imaginal discs is now their generally accepted designation.

It has been well established by numerous works that the imaginal discs are of hypodermal origin and some may appear in the embryo or very young larva. This conclusion is the result of the researches of Kunckel d'Herculais, Van Rees, Wahl, Ganin, Lowne, Pratt, and others.

The optic discs which concern us chiefly in this work are part of larger bilateral structures, which contain also the antennal and facial discs. These incompletely conical sacs were termed the "brain appendages" by Weismann. They arise in the late embryo or very early larva. It has been shown by Weismann, Lowne, and other workers on this phase of dipterous development that in the late embryo, the changes are such that the parts which give rise to the head of the adult become deeply invaginated, and in

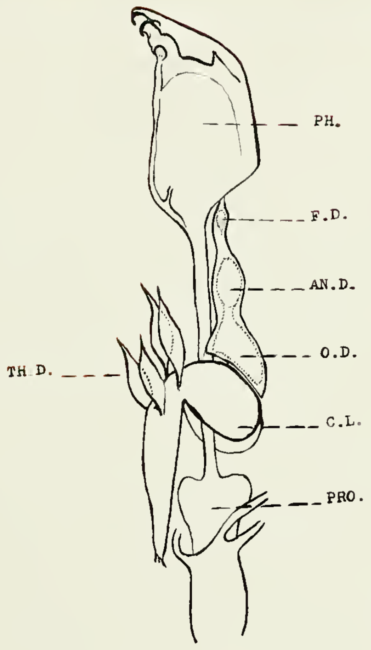

FIG.1

FIG. 1, Optic disc and adjacent parts of dissected larva, seen from left side. PH., pharynx; F.D., facial disc; AN.D., antennal disc; O.D., optic disc; TH.D., thoracic discs; C.L., cerebral lobes; PRO. proventriculus.

the larva these parts come to lie just in front of the cerebral ganglia of the larva. (Fig. 1.)

Lowne in his Fig. 7. which is a vertical longitudinal section through the newly-hatched larva shows that the optic disc arises as a dorsal evagination from the pharynx. The structure called the pharynx is really not a part of the alimentary canal, but is itself an invaginated portion of the head, into the base of which the oesophagus opens. From the standpoint of descriptive embryology there is still a problem whether the brain appendages arise in the embryo as paired or unpaired structures from the pharynx. But for our purposes there is no doubt about their paired nature in the larval stages.

These bilateral cone-shaped structures contain the chief cephalic discs, the optic, antennal and facial discs. The situation has been described in Musca by Hewitt (1908 p. 533.) and a study of larvae of Drosophila both by dissection and by section agree with his findings. His description follows: "The chief cephalic discs are contained in what at first appears to be a pair of cone-shaped structures in front of each of the cerebral lobes of the ganglion; the cone, however, is not complete. The outer sheath of each of these major cephalic imaginal rudiments is continued dorsally and joins the cellular structure (Weismann's ring) thus enclosing a triangular space which is a portion of the ventral sinus. These sheaths are continued anteriorly and are connected to the pharyngeal mass, and it is through this connecting strand of tissue that the discs are everted to form the greater part of the head of the nymph.

Immediately in front of the cerebral lobe is the so-called optic disc, which in its earlier stage is cup-shaped, but later it assumes a conical form, having a cup-shaped base adjacent to the cerebral lobe. The optic disc is connected to the cerebral lobe laterally by a stalk of tissue, the optic stalk which becomes hollow later, and it is through this stalk that the optic ganglion and associated structures contained in the cerebral lobe appear to evaginate when the final metamorphosis and eversion of the imaginal rudiments take place. The optic discs form the whole of the lateral regions of the head of the fly. The remaining portion of the head capsule of the fly is formed from two other pairs of imaginal rudiments, the antennal and facial discs. The antennal disc lies in front of and internal to the optic discs. ..... The facial discs are anterior to the antennal discs and extend to the anterior end of the conical structure containing these three pairs of major cephalic discs, which will form the major cephalic capsule."

It is impossible to understand the later development of the eye apart from the formation of the head. It has been indicated above that in the group of Diptera to which Drosophila belongs, the Brachycera, there is a curious retrograde development of the head in the late embryo, so that the larvae of these insects are spoken of as acephalous. The structures which form the head are invaginated in the larvae and are found in the thoracic segments of the larvae. The development of the head from these invaginated structures has been elucidated by the researches of Kowalevsky (1887), Van Rees (1888) and by Wahl (1915). This development

for convenience may be divided into two periods. The earlier of these two periods, which may be known as the cryptocephalic stage occurs in the late larval stage when the larva is quiescent and is undergoing the transition to the pupal stage, and in the early days of pupal life. The later period, which may be known as the phanerocephalic stage, occurs in the later stages of pupal life. It is the stage from the time of the complete eversion of the head up to the emersion of the imago.

It is during the cryptocephalic stage that the first definite arrangement of the cells of the optic disc are sufficiently differentiated to suggest future ommatidia. The cells are arranged in groups or columns. It is probably these groups which Viallanes (1882, p. 277) has called optogenic cells. It is not an easy task to determine the number of cells in each column. Lowne (1891 p. 546) says, "They ..... form four more or less distinct layers, a corneal layer, a series of bundles of fusiform cells beneath the corneal layer, a double layer of round cells, and an inner columnar layer." These cells become the later pseudocone cells, retinulae, pigment cells, and they give rise to the rhabdomes.

The above outline of the embryology of the compound eye and the histogenesis of the ommatidia serves as an orientation for the purpose of this phase of the work, the object of which was to determine the nature of the mechanism in the larva, from an embryological point of view, which results in a certain facet count in the adult. There are many gaps in the knowledge of the development of the ommatidia, which in so far as can be

seen at present must be filled in, for a solution of the problem, and for an answer to the inquiry of how the gene acts from an embryological point of view. From the structural side, there is no doubt that the facet reaction period occurs much earlier than it is possible to detect the earliest differentiation of anything similar to ommatidia.

Comparison of Optic Discs of Larvae raised at 17° C. and 27° C.: The facet reaction period occurs between the time when 32% and 45% of development has been completed, when the whole period of development is passed at any one temperature (Krafka 1920 p. 443). It seems reasonable to suppose that some process is going on at this time within the optic disc which determines the number of facets in the adult fly. By the method and technique described above, the larvae were studied in an effort to find some differential action of the two temperatures upon the optic disc, which results in the adult females of a count of 108 facets at 17° C. and 42 facets at 27° C. in the bar stock which was used for this work.

The appearance of the optic disc during this time is seen in Fig. 2. The wall which gives rise to the ommatidia consists of several layers of cells, and the cells seem to be all of the same sort. This same appearance was observed in the other major cephalic discs as well as in the thoracic discs. No difference was seen in optic discs from larvae of 17° and 27° killed during the facet reaction period, and no difference was seen between the optic discs and other imaginal discs of the same period. Further research, however, is needed on this point, and it must

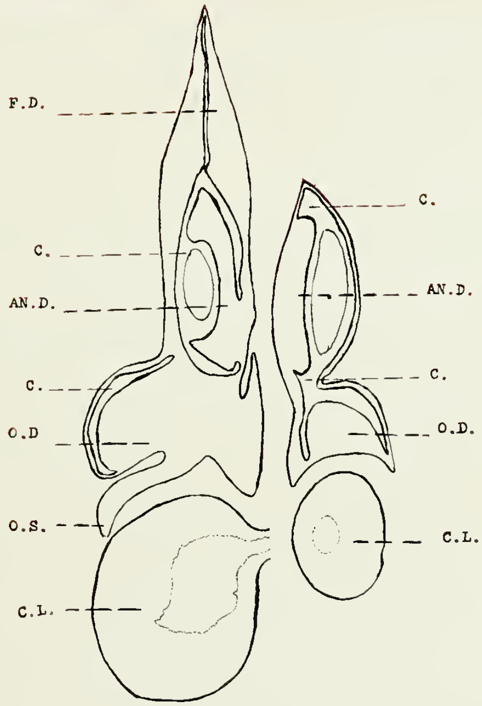

FIG.2

FIG. 2. Longitudinal Horizontal Section through optic disc in the same stage of development as Fig. 1. At left, a more dorsal section, at right, a more ventral section from same larva. F.D., facial disc; AN.D., antennal disc; O.D., optic disc; O.S., optic stalk; C.L., cerebral lobes; C., cavity of "brain appendages."

be reckoned with as a possibility that the process which takes place during the facet reaction period is not visible structurally and secondly that the determining reaction may not occur in the cells of optic discs but in some other tissue. It has been suggested that the determining reaction might occur in the cells of the optic ganglion.

It might be suggested here that for further inquiry into the nature of the mechanism in the larva which determines ommatidial number in the adult that a better technique is needed. A fixative of such nature that the mitotic figures of the imaginal discs will be preserved would show whether there is a differential rate in cell division at this time between the optic discs and the other imaginal discs. A suitable method for orientation of the larvae in the paraffin block is also to be desired.

The whole problem is further complicated by the fact that the optic disc gives rise not only to the ommatidia, but also to the side of the head. This may turn out to be an important consideration in the investigation of the embryological mechanism, for, since all the cells of the optic disc look pretty much alike, the facet reaction is not so apparent structurally, it will be no easy matter to determine which of the many cells of the optic disc are involved in the later production of ommatidia.

Finally it is suggested that in order to determine whether germinal and environmental (temperature) changes act in the same way to produce the adult character that determinations be made of the duration of the length of the facet reaction per-

iod in flies having the same facet count at some particular temperature but having different germinal constitutions. In the present state of knowledge, it is of little use to speculate what would be the meaning, on the one hand, if these two periods happened to be of the same duration, or, on the other hand, if they happened to be different.

III. The Effect of Temperature upon the Heterozygous Condition.

Introduction: It was pointed out above that one phase of the facet problem is an analysis of what is the nature and manner of action of temperature changes upon the heterozygous condition, and a comparison of such knowledge with what is known about the effect of temperature upon the homozygous condition.

The effect of temperature upon the heterozygous condition is especially desirable too from the purely genetic standpoint for the light that it might throw upon the problem of dominance.

This part of my study seeks to find out how temperature acts upon the heterozygous condition, how it differs from the homozygous condition, and how a certain gene acts in different combinations of its allelomorph. This study shows that there is a temperature at which a gene has its maximum effect in its dominance relation to one of its allelomorphs.

Materials and Methods: The particular stocks used in these experiments were secured from Doctor Charles Zeleny. The full stock is his 2054.1, which was established from a reverse mutation from low selected bar from bar 80 forked 1961.5. The low bar stock is his 1165.1, which has been selected for facet number in the low direction. This stock was used in the embryological work mentioned above. The ultra-bar stock is his 1214.1, a stock which was established from a single high male of 45 facets which appeared in his original ultra-bar stock.

Method of Mating: The method employed in these experiments was to mate 10 probable virgins of one stock with 10 males

of another stock in an 8-dram vial containing banana-agar food inoculated with yeast, and then to place the bottle at the experimental temperatures. After several days the parents were removed from the bottle and the F_1 females, since they only show the heterozygous condition, were counted for facet number. All flies which were counted were preserved.

Method of Counting: The flies were counted upon blackened paraffin in a Syracuse glass. The best slope for placing the flies was easily secured by chipping away the paraffin. The flies were placed upon the inclined slope of the paraffin and counted under the compound microscope with a Leitz 4 ocular and a Leitz 3 objective. The F_1 females of the full by bar cross gave rather high facet counts, and for this counting, the dorsal and ventral regions of the eye were counted separately and the results were added to get the facet count for each individual.

Methods of Securing the Series of Temperature: In this work the temperatures were chosen between 15° and 31° with an interval of two degrees. The temperatures 15° and 25° were secured by the use of the cool and warm rooms in the Vivarium Building. The rooms are kept constant by forcing air over brine coils which is then returned to the room. In addition to the brine in the warm room steam coils are present.

The temperatures 17° and 27° were secured by incubators converted for the purpose in the cool and warm rooms respectively.

The temperatures 19°, 21°, 23°, and 31° were maintained in aquaria fitted with temperature control. Twenty-nine degrees was secured in an incubator which was kept in Room 101 of the

Vivarium Building.

Methods of Tabulation: It has been shown by Zeleny (1920) that differences in facet number is not a good measure of the value of the temperature. This is readily seen by a few comparisons from counts in this work. The facet differences in low bar females for the temperature interval 15° to 23° is 66.2 facets and for the interval 23° to 31° it is 27.5. On the factorial basis the corresponding difference in factorial units is respectively 7.73 and 6.25 units. The better system is naturally the one which more nearly gives a 1:1 ratio for a similar temperature interval, in this particular instance 8°.

It is readily seen that the factorial system gives the better tabulation of the data than the facet counts. All facet counts were tabulated then on the factorial system as described by Zeleny (1920). The variation constants consequently are in terms of factorial units.

Sources of Error: Errors in this study may arise from fluctuating temperatures. The fluctuation was not the same in all cases. 17° and 27° were the most constant temperatures. The temperature records from these two incubators show a variation of 0.5°. 15° and 25° also show a variation of 0.5°. 19°, 21° and 23° were more variable. Temperature records taken of the food by a thermometer, graded in tenths of degrees, show that the 31° temperature varied from 31.3° to 32.7° -- at another time readings showed a variation from 31.3° to 31.7°. Similar tests on the 21° aquarium showed a variation from 21.1° to 21.9°. At another time, readings from this aquarium varied from 20.4° to

21.7°. Since it is not always possible to tell what the exact temperature was during the facet reaction period, there is room here for a slightly larger variation, than the temperature record might indicate. Nominal temperatures in accompanying tables and figures are to be considered with these remarks in mind.

Another source of error comes from the method of counting. It has been pointed out by previous workers that as the number of facets increase the percentage of error increases. The largest facet count in this work occurs in the cross between full and bar. Here, however, there is not the likelihood of there being a differential error in any direction. By a check made by counting 16 flies of full and bar cross at 23° it was found that a total count gave 4738 as the facet count. A recount of the same flies made nearly a week later gave a total count of 4797. Since the average count of all flies of this cross at this temperature showed an average of 300 facets, the personal error involved in the figures above is not very large.

There is another source of error which might be a factor in the ultra-bar by bar cross. When the ultra-bar is used as mother it may be possible that all the flies used were not virgins, with the result that some ultra-bar females may be included in counts of the F_1 females. The practice in all experiments was to use flies not older than 24 hours and several tests indicate that it is fairly safe to assume that females not older than 24 hours are virgin.

It was found that when the ultra-bar stock was used as the mother the F_1 females seemed to have a slightly higher facet

count. A definite test of this point was made. Reciprocal crosses of ultra-bar by bar were made at 27°. When ultra-bar was the mother 96 F_1 females gave a mean of -5.55 ± 0.11 on the factorial basis, while when ultra-bar was used as fathers, 120 F females gave -6.64 ± 0.09 as the mean. This is a difference of 1.1 factorial units. The probable error of this difference, calculated from the following formula:

$$E_D = \pm\sqrt{E_1^2 + E_2^2}$$

was found to be ± 0.14, which is nearly eight times the difference so that this difference is significant. Since all the crosses at all the temperatures were not made in the same direction the results are not so uniform as might be desired. In spite of the fluctuation in the temperatures, and in spite of the fact that all crosses were not made in the same direction, it is safe to say that the departure from the most correct results caused by these discrepancies is so slight as not to invalidate the conclusions drawn from the data.

The Effect of Temperature Upon the Homozygous Stocks: Seyster (1919) and Krafka (1920) showed that the number of facets decreases with increase in temperature in bar and ultra-bar races of Drosophila. This has become a commonplace of the effect of temperature on facet count. The rate of decrease is proportional to the number of facets within any given stock, so that we are dealing with an instance of "the compound interest law" (Mellor 1919 p. 56). The rate of decrease of facet number differs

for each of the stocks used. For the bar and ultra-bar stock which were used in these experiments it is respectively 10.7% and 9.5% per degree for the interval from 15° to 27° (table 3). The same general decrease is true for the heterozygotes which will be taken up below. We may state in general then that the rate of decrease in facets for homozygous and heterozygous flies is an exponential function of the temperature. The results of the experiments on the bar and ultra-bar stocks are summarized in tables 1 and 2, 4 and 5.

The effect of temperature upon flies heterozygous for full and ultra-bar: The results of these experiments are summarized in tables 6 and 7 and fig. 3. It can be readily seen from figure 3 that the general slope of the line representing the F_1 females is more like ultra-bar than it is like full. Also from table 3 of the temperature coefficients, it is obvious that the percentage decrease per degree is of the same order as that of the ultra-bar parent rather than the full parent. A word may be said here about the manner of calculating the temperature coefficients. The method followed is that used by Doctor Zeleny in the manuscript of a paper which he has kindly allowed me to use, and which may be illustrated here by the use of an example.

The difference between the logarithms of the facet counts at 15° and 29° and divided by 14 -- the number of degrees of temperature difference -- is 0.034094, the natural number of which is 1.082. This means that the average rate of change per degree between 15° and 29° is 8.2%.

By a comparison of the temperature coefficients of full,

TABLE 1.

Temperature °C.	Number of flies	Arithmetical mean	Mean	Standard Deviation
15	64	125.6	+ 8.16 ± 0.09	± 1.07 ± 0.06
17	50	108.3	+ 6.53 ± 0.10	± 1.00 ± 0.07
19	71	79.1	+ 3.25 ± 0.11	± 1.41 ± 0.08
21	60	76.9	+ 3.04 ± 0.14	± 1.66 ± 0.10
23	78	59.4	+ 0.43 ± 0.15	± 1.98 ± 0.11
25	84	49.5	- 1.43 ± 0.13	± 1.76 ± 0.09
27	115	42.0	- 3.13 ± 0.14	± 2.28 ± 0.10
29	57	30.6	- 6.14 ± 0.17	± 1.85 ± 0.12
31	54	31.9	- 5.82 ± 0.14	± 1.51 ± 0.10

Summary of Experiments on bar females. The last two columns are expressed in factorial units.

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TABLE 2.

Classes in factorial units	Classes in facets	Distribution of flies at each temperature.								
		15°	17°	19°	21°	23°	25°	27°	29°	31°
-10.93	18-19								3	
- 9.93	20-21								0	
- 8.93	22-23							1	1	3
- 7.93	24-26							2	5	6
- 6.93	27-29							8	17	7
- 5.93	30-32					1		10	13 *	11 *
- 4.93	33-35					0	1	10	9	17
- 3.93	36-39					2	4	22	4	8
- 2.93	40-43					4	8	14 *	4	2
- 1.93	44-48					4	8	16	1	
- 0.93	49-53				1	11	18 *	18		
+ 0.07	54-59			2	1	18 *	20	12		
+ 1.07	60-65			3	11	17	15	1		
+ 2.07	66-72			20	12	12	7	1		
+ 3.07	73-80			19 *	12 *	6	3			
+ 4.07	81-88		2	15	13	2				
+ 5.07	89-97	1	7	7	5	0				
+ 6.07	98-107	2	12	4	4	1				
+ 7.07	108-118	15	25 *	1	1					
+ 8.07	119-131	25 *	3							
+ 9.07	132-145	14	1							
+10.07	146-160	7								
	TOTALS:	64	50	71	60	78	84	115	57	54

The data of table 1. on bar females to show distribution at the various temperatures.

* The class which contains the mean value.

TABLE 3.

Temperature Interval	LFB	LFB by Ultra-bar	Ultra-bar	Full by Ultra-bar	Full	LFB by Full
15° - 23°	9.8	8.4	11.6	8.9	2.4	2.9
15° - 25°	9.7	8.4	11.4	6.3	2.5	1.5
15° - 27°	9.5	6.4	10.7	8.0	2.5	1.9
15° - 29°	10.6	8.2	10.4	8,2	2.4	7.5
15° - 31°	8.6	8.3	9.1	7.9	2.2	7.2
17° - 25°	10.2	6.8	10.6	6.4	2.4	0.7
17° - 27°	9.9	6.7	10.2	8.6	2.5	1.2
17° - 29°	11.1	8.8	10.2	8.7	2.3	7.9
17° - 31°	9.1	8.7	8.7	8.5	2.2	7.3
19° - 27°	8.5	6.7	8.6	9.6	2.3	1.2
19° - 29°	9.9	7.0	8.7	9.5	2.2	9.3
19° - 31°	7.9	7.1	7.2	8.9	2.0	8.4
21° - 29°	12.2	6.9	9.4	8.9	2.4	10.8
21° - 31°	9.2	7.2	7.6	8.4	2.2	9.4
23° - 31°	8.2	6.9	7.1	7.0	2.1	11.4
AVERAGES:	9.6	7.5	9.4	8.2	2.3	

Temperature coefficients, expressed as percents of change per degree Centigrade for 8° intervals.

TABLE 4.

Temperature °C.	Number of flies	Arithmetical mean	Mean	Standard Deviation
15	26	69.9	+ 1.86 ± 0.27	± 2.29 ± 0.19
17	50	56.0	- 0.19 ± 0.18	± 2.00 ± 0.13
19	97	40.0	- 3.64 ± 0.16	± 2.30 ± 0.11
21	58	36.1	- 4.52 ± 0.17	± 1.90 ± 0.12
23	73	29.1	- 6.75 ± 0.18	± 2.26 ± 0.13
25	81	24.5	- 8.35 ± 0.15	± 2.06 ± 0.11
27	66	20.7	-10.02 ± 0.21	± 2.49 ± 0.15
29	57	17.6	-11.67 ± 0.21	± 2.39 ± 0.15
31	43	17.4	-11.73 ± 0.26	± 2.49 ± 0.18

Summary of Experiments on ultra-bar females. The last two columns are expressed in terms of factorial units.

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TABLE 5.

Classes in factorial units	Classes in facets	Distribution of flies at temperatures indicated.								
		15°	17°	19°	21°	23°	25°	27°	29°	31°
-18.93	8									1
-17.93	9							1		0
-16.93	10							0	2	1
-15.93	11							0	3	2
-14.93	12							3	5	2
-13.93	13+					1	1	1	1	2.5
-12.93	15+					1	1	4	9	9.5*
-11.93	16-17					0	4	9	7	4
-10.93	18-19					0	8	9	12*	8
- 9.93	20-21					7	7	14*	9	4
- 8.93	22-23			1		6	13	6	4	7
- 7.93	24-26			3	4	12	23*	10	4	1
- 6.93	27-29			7	6	11*	14	5	1	1
- 5.93	30-32		1	13	9	17	5	3		
- 4.93	33-35		0	9	11	7	2	0		
- 3.93	36-39		0	23	12*	6	2	1		
- 2.93	40-43		4	10*	7	3	0			
- 1.93	44-48	4	9	17	6	2	1			
- 0.93	49-53	1	13	5	2					
+ 0.07	54-59	5	10*	5	1					
+ 1.07	60-65	5	8	2						
+ 2.07	66-72	5*	4	2						
+ 3.07	73-80	6	2							
+ 4.07	81-88	3	2							
+ 5.07	89-97	2	1							
+ 6.07	98-107	1								
+ 7.07	108-118	1								
	TOTALS:	33	54	97	58	73	81	66	57	43.

The data of table 4 on ultra-bar females to show distribution at each temperature.

* The class which contains the mean value.

TABLE 6.

Temperature °C.	Number of flies	Arithmetical mean	Mean	Standard Deviation
15	90	89.1	+ 4.55 ± 0.11	± 1.55 ± 0.08
17	54	81.4	+ 3.51 ± 0.21	± 2.31 ± 0.15
19	83	73.7	+ 2.49 ± 0.11	± 2.29 ± 0.12
21	100	59.0	+ 0.32 ± 0.13	± 1.89 ± 0.09
23	86	45.1	- 2.43 ± 0.18	± 2.43 ± 0.13
25	122	48.6	- 1.63 ± 0.14	± 2.31 ± 0.10
27	137	35.5	- 4.62 ± 0.10	± 1.65 ± 0.07
29	98	29.7	- 6.66 ± 0.18	± 2.60 ± 0.13
31	53	26.3	- 7.71 ± 0.22	± 2.45 ± 0.16

Summary of experiments of F_1 females of full x ultra-bar cross. The last two columns are expressed in terms of factorial units.

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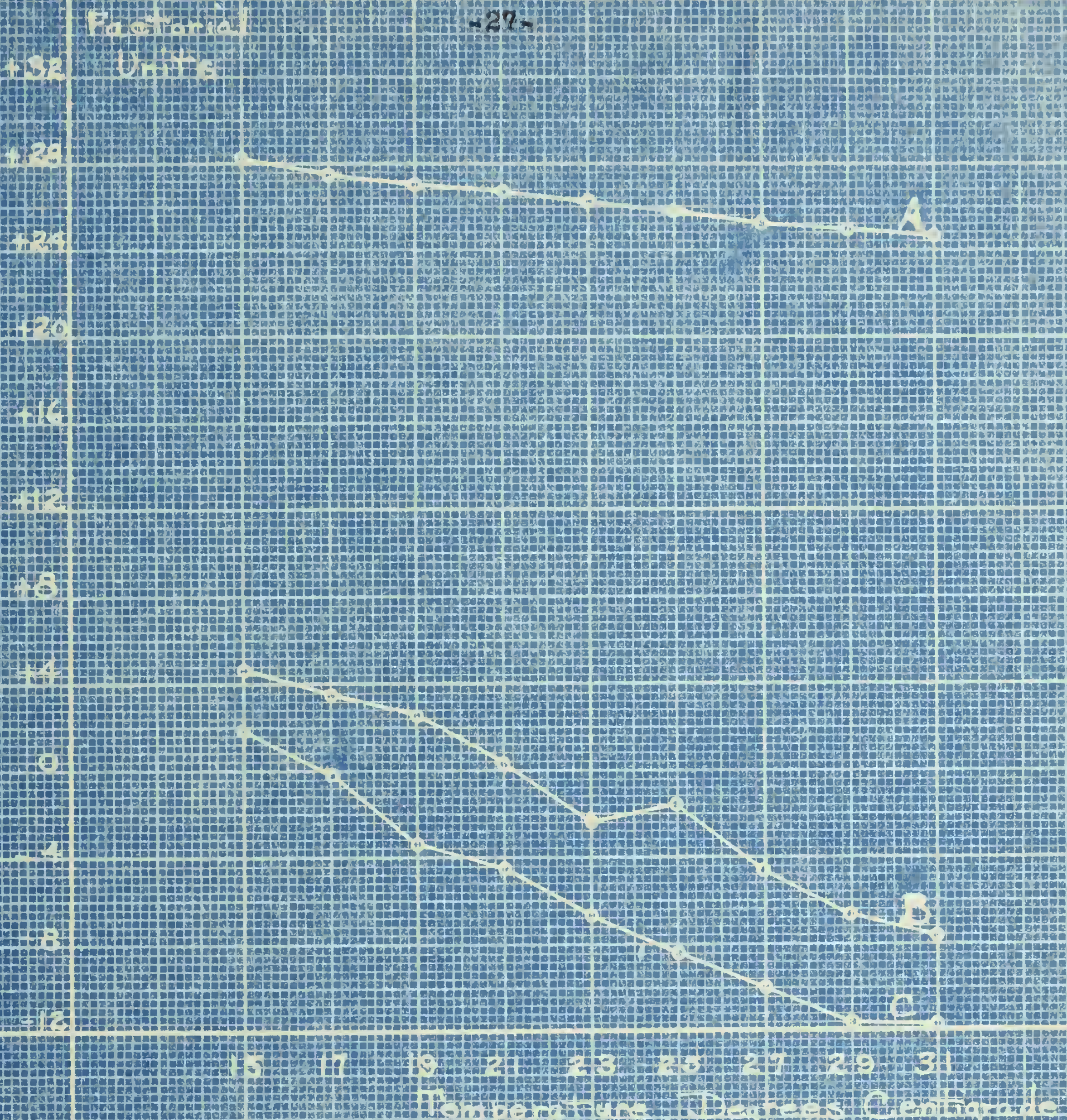
TABLE 7.

Classes in factorial units	Classes in facets	Distribution of flies at temperatures indicated. 15°	17°	19°	21°	23°	25°	27°	29°	31°
-15.93	11									1
-14.93	12									0
-13.93	13+								.5	.5
-12.93	15+								.5	.5
-11.93	16-17						1		1	2
-10.93	18-19						0		10	2
- 9.93	20-21						0		4	4
- 8.93	22-23					1	0	2	5	5
- 7.93	24-26					3	1	8	8	8 *
- 6.93	27-29					2	0	11	28	9
- 5.93	30-32					2	2	19	14 *	13
- 4.93	33-35				1	4	4	26	6	6
- 3.93	36-39				2	19	18	44 *	10	1
- 2.93	40-43		2	1	5	12	15	15	4	
- 1.93	44-48		0	1	9	14 *	22 *	8	6	
- 0.93	49-53		1	7	12	11	24	3	1	
+ 0.07	54-59		3	7	26 *	7	19	1		
+ 1.07	60-65	3	4	14	21	8	9			
+ 2.07	66-72	7	5	14	16	2	2			
+ 3.07	73-80	12	10	12 *	6	1	3			
+ 4.07	81-88	22	10 *	16	0		2			
+ 5.07	89-97	25 *	9	2	1					
+ 6.07	98-107	13	7	3	0					
+ 7.07	108-118	5	2	5	1					
+ 8.07	119-131	3	1	1						
	TOTALS:	90	54	83	100	86	122	137	98	53.

The data of table 6 showing the distribution of the females of full x ultra-bar cross.

* The class which contains the mean value.



- Figure 3 -

The Effect of Temperature upon full, ultra-bar, and heterozygates

Curve A, for full
Curve B, for heterozygates
Curve C, for ultra-bar

ultra-bar, and flies heterozygous for these factors, we may draw the conclusion that when one full gene is replaced by an ultra-bar gene, the resulting system is more like ultra-bar than it is like full with regard to the effect of temperature upon it.

The Effect of Temperature upon Flies Heterozygous for full and bar: The results of these experiments are summarized in tables 3, 8, and 9, anf fig. 4. From the figure it can be readily seen that the slope of the line representing the heterozygotes follows that of full much more closely than that of bar up to 27^{0}. From table 3 it can be seen also that the temperature coefficients are more like that of full than that of bar. It follows then in this cross that the replacement of a full by a bar gene gives a protoplasmic system which in its response to changes in temperature is more nearly like the full stock than it is like bar.

The Effect of Temperature upon Flies Heterozygous for bar and ultra-bar: Tables 3, 10, and 11, and fig. 5 summarize the results of these experiments. By a comparison of the temperature coefficients as shown in table 3 it is seen that on the whole flies heterozygous for these two genes are more like flies homozygous for ultra-bar than they are like bar.

In this cross we see that the replacement of a bar gene by an ultra-bar gives a system which in its temperature relations is more like the ultra-bar stock than it is like bar.

Results of the Study of these Three Crosses: From the study of these three sets of heterozygotes we may state generally that the replacement of a gene by another in a homozygous stock

TABLE 8

Temperature °C.	Number of flies	Arithmetical mean	Mean	Standard Deviation
15	26	378.6	+ 18.92 ± 0.24	± 1.81 ± 0.17
17	50	342.5	+ 18.90 ± 0.12	± 1.21 ± 0.08
19	5	334.2		
21	25	311.8	+ 16.91 ± 0.29	± 2.11 ± 0.21
23	22	300.1	+ 16.43 ± 0.28	± 1.96 ± 0.20
25	36	324.9	+ 17.46 ± 0.25	± 2.19 ± 0.18
27	50	303.6	+ 16.61 ± 0.23	± 2.46 ± 0.16
29	77	137.2	+ 7.94 ± 0.37	± 4.84 ± 0.26
31	39	127.0	+ 7.48 ± 0.43	± 3.98 ± 0.30

Summary of experiments on the full x bar cross. The last two columns are expressed in factorial units.

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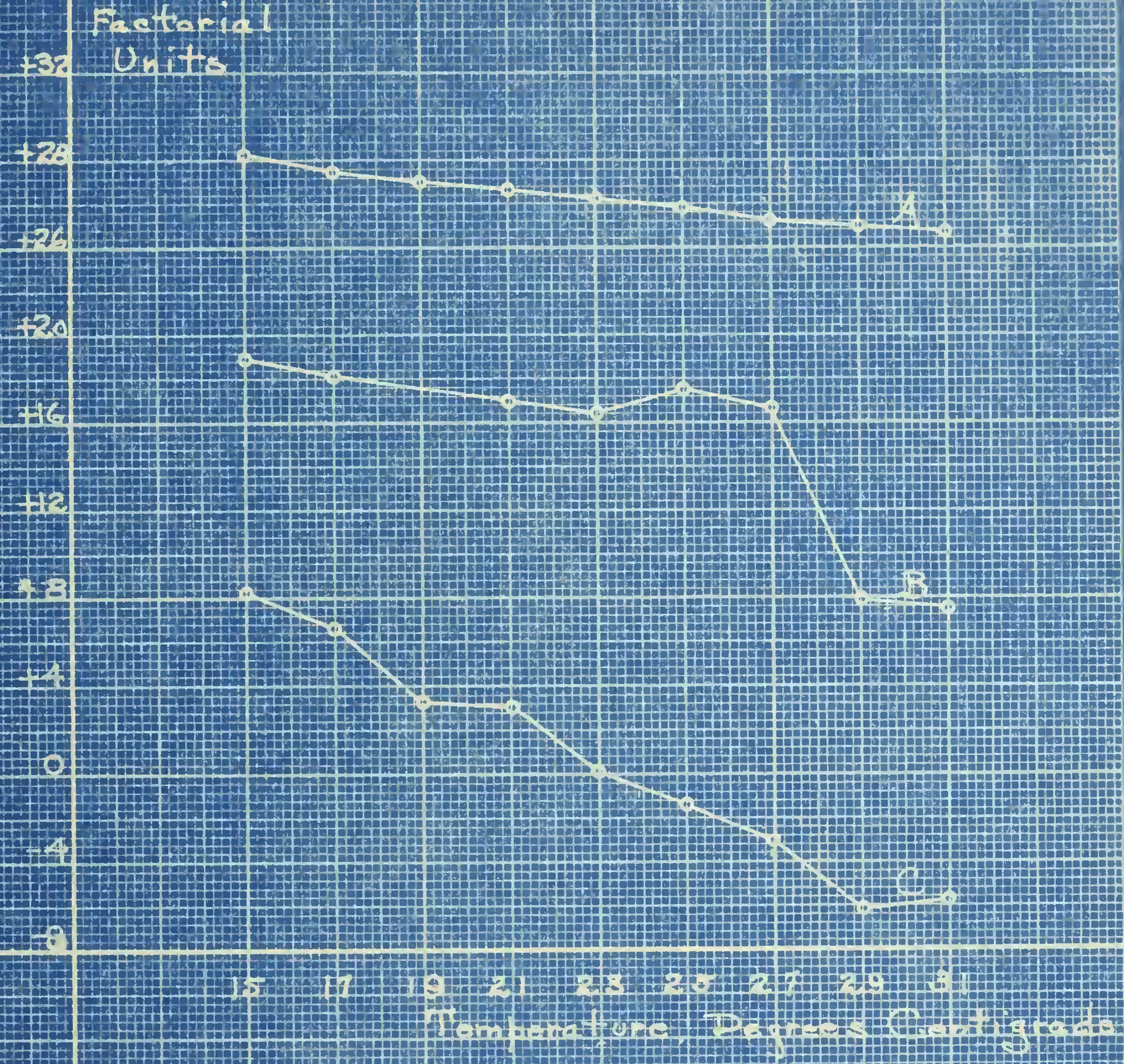
TABLE 9.

Classes in factorial units	Classes in facets	Distribution of flies at each temperature								
		15°	17°	19°	21°	23°	25°	27°	29°	31°
- 1.93	44-48								3	
- 0.93	49-53								0	2
+ 0.07	54-59								0	0
+ 1.07	60-65								5	1
+ 2.07	66-72								5	2
+ 3.07	73-80								3	3
+ 4.07	81-88								8	1
+ 5.07	89-97								0	3
+ 6.07	98-107								5	5
+ 7.07	108-118								9	1
+ 8.07	119-131								5	4*
+ 9.07	132-145								2*	5
+10.07	146-160								7	7
+11.07	161-177							2	6	0
+12.07	178-196					1		3	3	1
+13.07	197-217				3	2	2	2	4	0
+14.07	218-240				1	1	3	4	6	2
+15.07	241-265	1	2		2	1	2	5	1	2
+16.07	266-293	0	3	1	5	4	5	2	3	
+17.07	294-324	5	12	1	5*	5*	4	12*	2	
+18.07	325-358	7	10*	1	1	4	8*	8		
+19.07	359-396	4*	22	2	5	4	6	8		
+20.07	397-438	5	0		3		4	4		
+21.07	439-484	1	1				2			
+22.07	485-535	2								
+23.07	536-591	1								
	TOTALS:	26	50	5	25	22	36	50	77	39

The data of table 8, arranged to show the distribution of F_1 females of bar x full cross.

* The class which contains the mean value.



- Figure 4 -

The Effect of Temperature upon full, bar, and heterozygates —

Curve A, for full.
Curve B, for heterozygates.
Curve C, for bar.

TABLE 10.

Temperature °C.	Number of flies	Arithmetical mean	Mean	Standard Deviation
15	50	63.2	+ 0.89 ± 0.17	± 2.55 ± 0.17
17	72	57.1	- 0.07 ± 0.19	± 2.34 ± 0.13
19	71	40.6	- 3.42 ± 0.18	± 2.21 ± 0.13
21	98	35.4	- 4.75 ± 0.16	± 2.29 ± 0.11
23	76	30.3	- 6.43 ± 0.21	± 2.71 ± 0.15
25	63	28.1	- 6.95 ± 0.13	± 1.57 ± 0.09
27	83	29.9	- 6.34 ± 0.12	± 1.66 ± 0.08
29	102	20.8	-10.37 ± 0.23	± 3.41 ± 0.16
31	55	17.7	-11.88 ± 0.23	± 2.45 ± 0.16

Summary of data of the bar x ultra-bar cross. The last two columns are expressed in factorial units.

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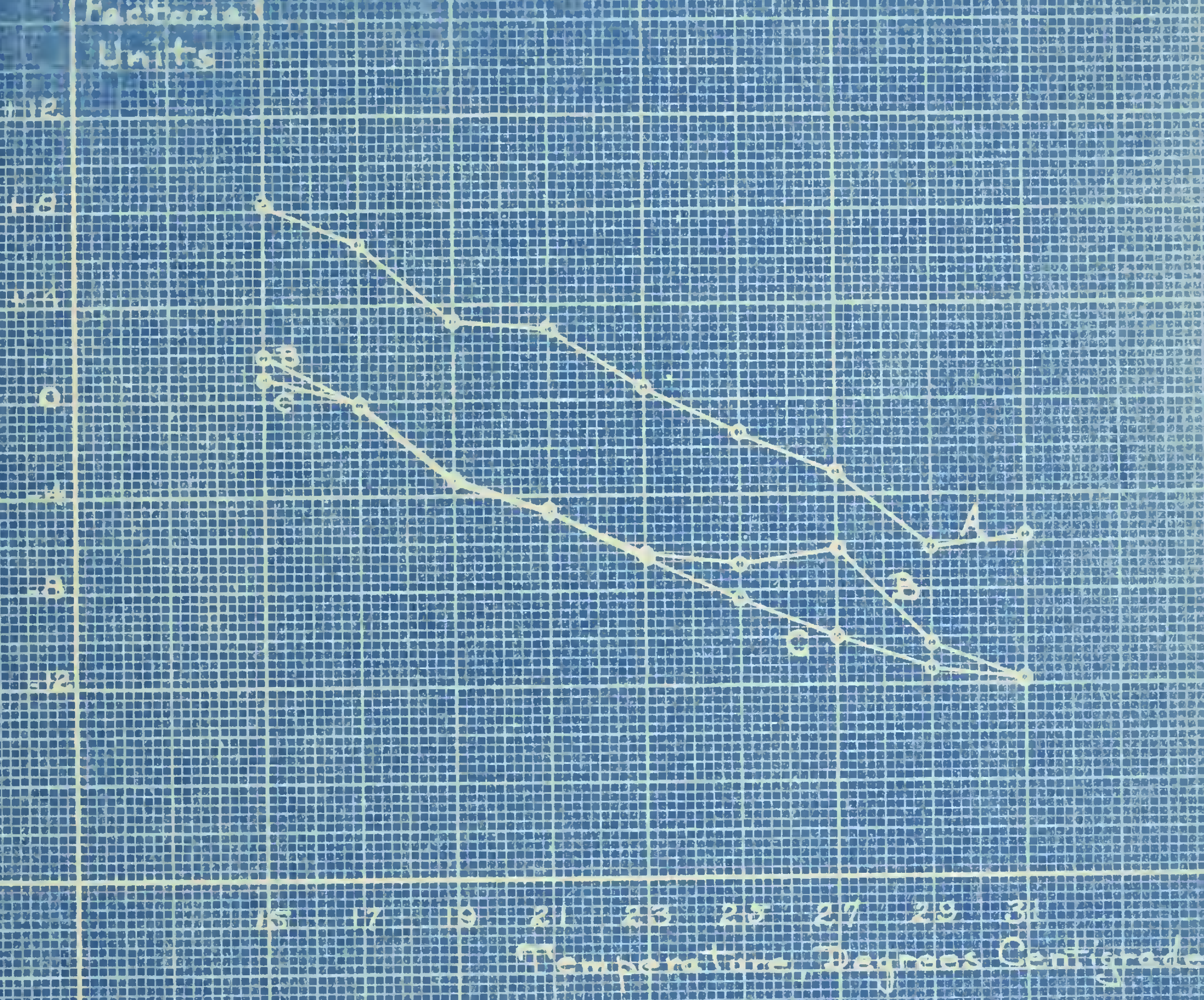
TABLE 11.

Classes in factorial units	Classes in facets	Distribution of flies at each temperature								
		15°	17°	19°	21°	23°	25°	27°	29°	31°
-18.93	8								1	
-17.93	9								0	1
-16.93	10								2	2
-15.93	11								3	3
-14.93	12								3	3
-13.93	13+								6.5	4
-12.93	15+								8.5	7
-11.93	16-17					2		1	15	8
-10.93	18-19					2		0	13	12*
- 9.93	20-21				1	7	3	1	19*	7
- 8.93	22-23			1	6	5	7	2	10	3
- 7.93	24-26			0	5	8	14	18	8	5
- 6.93	27-29	1	2	7	9	16	19*	17	2	
- 5.93	30-32	0	0	7	18	15*	11	24*	1	
- 4.93	33-35	1	1	7	13*	7	4	11	3	
- 3.93	36-39	0	3	12	20	6	3	5	1	
- 2.93	40-43	3	3	14*	11	1	2	3	2	
- 1.93	44-48	2	10	9	10	3		0	1	
- 0.93	49-53	8	12	7	2	2		1	3	
+ 0.07	54-59	7	10*	5	1	0				
+ 1.07	60-65	7*	9	2	1	1				
+ 2.07	66-72	7	15		1	1				
+ 3.07	73-80	5	5							
+ 4.07	81-88	7	2							
+ 5.07	89-97	2								
+ 6.07	98-107									
	TOTALS	50	72	71	98	76	63	83	102	55

The same data as table 10, arranged to show the distribution of F_1 females of bar x ultra-bar cross.

* The class which contains the mean value.



- Figure 5 -

The Effect of Temperature upon bar, ultra-bar, and heterozygotes.

Curve A - for bar
Curve B - for heterozygotes
Curve C - for ultra-bar

gives a result which in its responses to changes in temperature from the standpoint of rate of facet decrease per degree Centigrade is always like one of the parents and is not intermediate. There are certain deviations from this general statement which may be taken up here. They are readily apparent by a study of figs. 3, 4, and 5. It is seen that for each cross there is a place in the temperature scale where an increase in temperature causes an increase in facet count, which is just the reverse of the usual condition. Is this due to an experimental error? The chief error which might result in such an increase would probably come from fluctuation in the temperatures, and furthermore the temperature interval is only 2°. The force of this probably explanation is greatly reduced when we consider that the increase occurs only in the heterozygous flies, not in the homozygotes, that they occur about the same place in the temperature range and furthermore 25° and 27° are rather constant temperatures. It should be pointed out also that the average rate of increase per degree for the interval is rather uniform. It varies between 3% and 4%. Can this increase be explained from the standpoint of the genes involved? It is suggestive that the increase occurs in the flies heterozygous for full in the two crosses where full is involved at 23° to 25°. Is this due to the Presence of the full factor? In the third cross the increase is one of 3% per degree between 25° and 27°. It may be seen from the curve, however, that the upward trend in the curve begins somewhat earlier than 25°. Here again is this deviation to be explained by some special effect of the temper-

atures involved upon a particular protoplasmic system heterozygous for bar and ultra-bar?

Another deviation is the steep drop in the curve (fig. 4) from 27° to 31°, in flies heterozygous for full and bar. The rate of decrease for this interval is on the average one of 24.3% per degree. What is the meaning of this great break in the curve? It is apparent that somewhere shortly above 27° the mechanism for facet formation produced by a full and a bar factor in the same fly is hampered, sometimes swinging more nearly to the bar condition, sometimes more nearly approaching the full condition.

Heterozygous flies are practically always intermediate in facet count between their homozygous parents. There are three points, however, in the present data which form exceptions to this rather universal rule. These three exceptions occur in the bar by ultra-bar cross, one is at 15° and the others at 21° and 31°. The differences at 21° and 31° are rather small and are probably not significant. At 15° the heterozygous flies, however, are nearly 7 facets lower than the homozygous ultra-bars at the same temperature. This is probably due to some change which has occurred in the ultra-bar stock. Some of the ultra-bar flies at 15° were raised later than the other flies, which would explain why the effect is produced at 15° and not at other points along the temperature range. One result of this irregularity is that at these points, 15° and 21° the dominance coefficient af ultra-bar over bar is more than 100. A discussion of dominance coefficients will now be taken up.

The Effect of Temperature upon Dominance: In the bar series of multiple allelomorphs, flies heterozygous for the various genes are intermediate in facet count between their parents except for the exceptions mentioned above. It is thus possible to get an expression for the degree to which the heterozygous flies approach one or the other parent in its number of facets. This expression is the coefficient of dominance and is calculated directly from the facet values rather than from the factorial unit values. The following method devised by Doctor Zeleny (1920 p. 308) is used in this work for the calculation of the coefficient of dominance:

$$C_D = \frac{AA - AA'}{AA - A'A'} \times 100$$

In this formula as applied to the present work AA and A'A' are the mean values of facet counts of the homozygous stock while AA' is the mean value of the facet count of heterozygous flies.

The coefficients of the three crosses for the nine temperatures which were used in the experiment are given in table 12 and the dominance coefficient plotted as a function of temperature is seen for the three series of heterozygotes in fig. 6.

It is seen in general that near 27° there is a low point for the dominance of the more dominant gene, and that from this critical temperature, dominance increases in both directions. This is not so apparent for the dominance of ultra-bar over full at temperatures below 27°, and makes the only probable exception to the general statement made above. It should be stated in this

TABLE 12.

Temperature °C.	Ultra-bar over full	Ultra-bar over Barr	Bar over Full
15	97.8	112.0	69.0
17	97.6	98.3	70.2
19	95.8	98.5	66.5
21	97.1	101.7	68.3
23	97.9	96.0	66.6
25	96.6	85.6	60.1
27	97.8	56.8	60.2
29	98.2	75.4	83.5
31	98.6	97.8	84.9

Coefficients of dominance of the more dominant gene in each of the three crosses.

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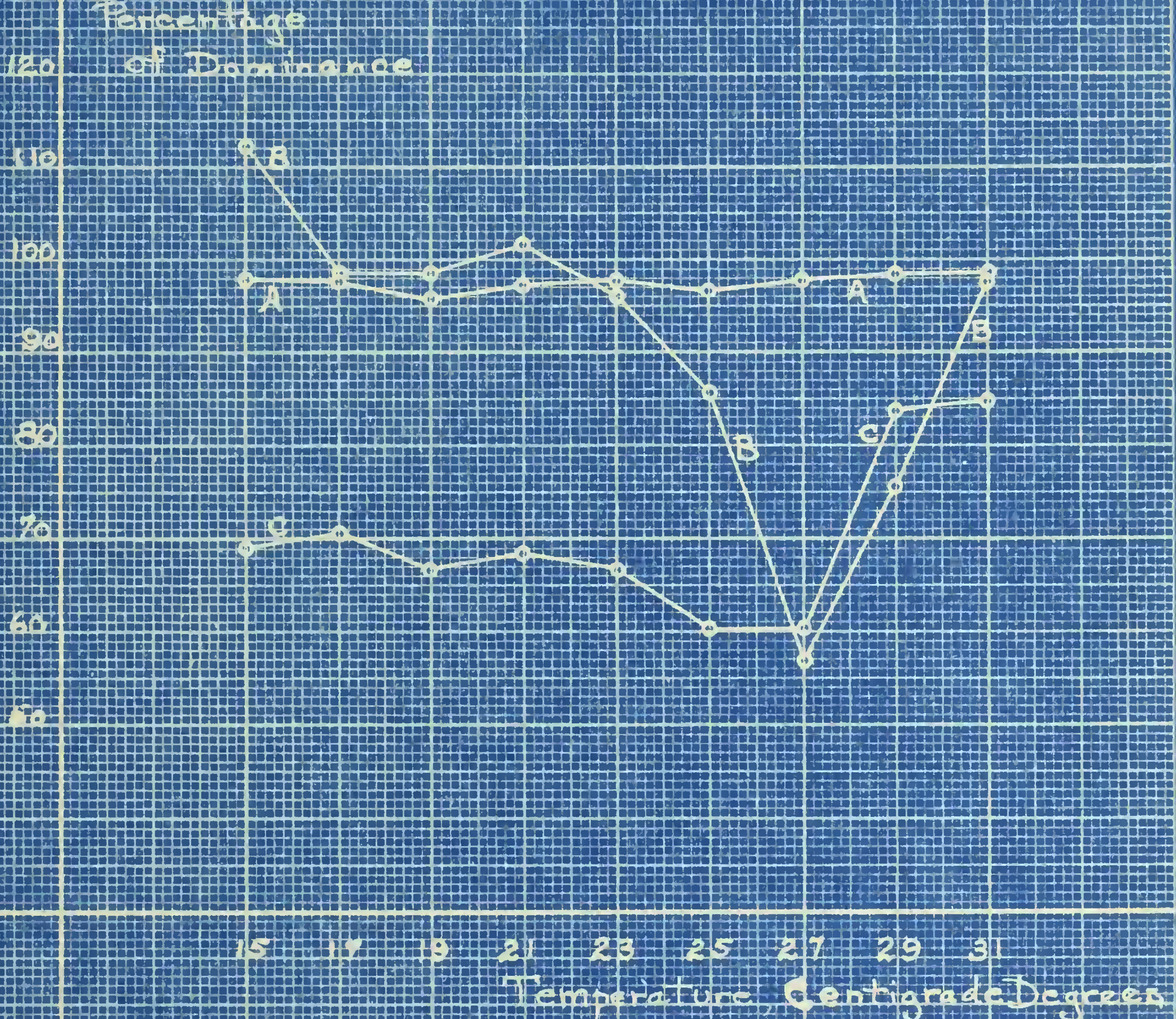

Figure 6

The Effect of Temperature upon Dominance.

Curve A- Ultra-bar over full
Curve B Ultra-bar over bar
Curve C Bar over full

connection that unpublished data of Doctor Zeleny's on a cross between full and ultra-bar, involving stocks different from the full and ultra-bar used for these experiments, and which he has allowed me to use show that the dominance of ultra-bar over full decreases at temperatures below 27°. The relation of dominance of the less dominant gene to temperature is merely the reverse of that for the more dominant gene. And curves showing this relation would in each case merely be the mirror image of its corresponding curve of fig. 6. This result follows by necessity from the manner of calculation.

It is interesting that near 27° is a critical temperature for change in the dominance relations between two genes, especially since some other physiological processes show a similar sensitivity. It is stated by Loeb and Northrop (1917) that growth is no longer accelerated above 27.5°. Krafka's data (1920 p. 426) shows that near 29° there is a point where velocity of development of Drosophila is no longer accelerated. Plough (1917 p. 163) in his work on the effect of temperature upon crossing-over shows that there is a sharp rise in the percentage of crossing-over in the second chromosome near 27°. He points out the similarity between his results and the results which physiologists obtain when they subject muscle to varying temperatures under constant stimulation. There is a maximum for the amount of contraction at about 28°.

It is highly suggestive that these several diverse processes should be sensitive to about the same degree of temperature. One would like to say that this similarity in response is more than mere coincidence, and that there is some connection.

If they are really related, we are probably safe in concluding that the explanation of the underlying cause will be found only when protoplasm as a colloidal system is more thoroughly understood than at present.

Nature of Dominance: Upon the rediscovery of Mendel's law in 1900, much was made of the principle of dominance, and dominance was at first stated as one of the basic principles of Mendelism. It soon became apparent in both plants and animals that sometimes dominance is not complete and that the heterozygote is intermediate in the expression of the pair of contrasting factors involved in the cross. Classic examples of this intermediate condition in the heterozygote are the common garden four-o'clock among plants and the case of the blue Andalusian fowl among animals. Heterozygotes in these experiments show this phenomenon of imperfect dominance. The problem of what constitutes dominance is further complicated in this work by the fact that accessory factors effect the expression of the genes. It is quite clear, however, that the intermediate condition is not due to accessory factors. One reason for the selection of the particular full and bar stocks which were used for these experiments, was the fact that the full arose as a reverse mutation from the bar stock. It follows then that these two stocks are similar for whatever accessory factors are present, provided, of course, that no mutation has since occurred in them which acts as an accessory factor on facet number. It follows from this that whatever conclusion is reached about the nature of dominance would follow irrespective of whatever accessory

factors might be involved.

We may summarize the conceptions of dominance which have been held as follows: DeVries (1902) held that the racially older characters were the dominant ones. Bateson (1914) seems to have held a similar view, due to the fact that practically all of the early mutations were recessives. This view is now no longer tenable. Another view of dominance is that favored by Davenport (1910) and Castle (1912). According to this view dominance is an attribute of the factor or determiner and variation in dominance is in large part merely the variation in the power of the gene to express itself in ontogeny. Another view of dominance is that of East (1912) and Emerson (1912) who think of dominance not as an attribute of the character but as White (1914) puts it, the "result of the activities of one or more specific factors, plus the modifications produced by the whole factorial organic complex, (all the other factors concerned in the organism's heredity) and by the external environment."

These experiments show that a factor may manifest itself in several ways, and the nature of dominance of each manifestation of the gene should probably be considered separately. The manner of response of ultra-bar is as much a part of the expression of the gene as is the number of facets in the adult fly. From this point of view it is seen that ultra-bar is completely dominant over full in its response to changes of temperature. In other words, the rate of change of facet decrease, in flies heterozygous for full and ultra-bar, with increase in temperature is of the same type as flies homozygous for ultra-bar and not like those homozygous for full. It happens also that

in facet count the heterozygotes are very close to ultra-bar rather than full.

In this connection the full by bar cross is very illuminating. At the lower temperatures the response of the heterozygous system is of the same order as full, but the coefficient of dominance of the facet counts show that bar is the more dominant gene. It is in this cross, as was pointed out above, that near 27° there is an abrupt drop in the curve (fig. 4) and the rate of change of facet decrease of this cross (table 3) may possibly mean that the protoplasmic system is more like bar, not only in facet count, but also in the manner of its response to these higher temperatures.

Hoge (1915) showed that factor A, a sex-linked character for the reduplicated legs in Drosophila was dominant at the lower temperatures. Roberts (1918) found in his study of vestigal wing, that when flies were raised in an incubator which ranged from 26.7° C. to 35.7° C. these temperatures increased the size of the wing. And then there is the case of Primula sinesis which at lower temperatures produces red flowers, but above 30° C. produces white flowers. From the standpoint of the present study it would be of interest to know at what temperature the transition takes place; whether the critical temperature for this change might agree with the critical temperature (27° C.) for changes in dominance brought out by the present study.

We conclude then that a gene may express itself in several ways. It may be more dominant in some of its manifestations and less dominant in others, relative to

course, to its allelomorph. And the changes in temperature may affect these several manifestations of the same gene in different ways.

A precise statement of the relation between allelomorphs which constitutes dominance is probably dependent upon a knowledge of the colloidal chemistry of the cell, and also upon a knowledge of the physiology of development. This opens up the whole question of embryonic differentiation which is still among the most mysterious of all organic processes.

Variability of Homozygotes and Heterozygotes: By the method of tabulation of results which is used in this paper, the standard deviations may be used directly as coefficients of variation.

In a comparison of the variability of the heterozygotes with the homozygotes it is found (table 13) that in the bar by ultra-bar cross the heterozygotes are distinctly more variable than either of the parents. In the two crosses where full is involved, the variability of full is not given. In the full by ultra-bar cross the data suggest that the variability on the whole is very similar to that of ultra-bar. In the bar by full cross, the variability is higher than that for bar.

With regard to the effect of temperature upon the variability of the five sets of flies, there is no general agreement. The variability of bar indicates that variability increases with temperature. It may further be pointed out that for bar the variability uniformly is lower than the rest of the flies which can readily be explained by the fact that bar has been selected for

TABLE 13.

Temperature °C.	Bar	Ultra-Bar	Bar x Ultra bar	Bar x Full	Full x Ultra-bar
15	±1.07±0.06	±2.29±0.19	±2.55±0.17	±1.81±0.17	±1.55±0.08
17	±1.00±0.07	±2.00±0.13	±2.34±0.13	±1.21±0.08	±2.31±0.15
19	±1.41±0.08	±2.30±0.11	±2.21±0.13		±2.29±0.12
21	±1.66±0.10	±1.90±0.12	±2.29±0.11	±2.11±0.21	±1.89±0.09
23	±1.98±0.11	±2.26±0.13	±2.71±0.15	±1.96±0.20	±2.43±0.13
25	±1.76±0.09	±2.06±0.11	±1.57±0.09	±2.19±0.18	±2.31±0.10
27	±2.28±0.10	±2.49±0.15	±1.66±0.08	±2.46±0.16	±1.65±0.07
29	±1.85±0.12	±2.39±0.15	±3.41±0.16	±4.84±0.26	±2.60±0.13
31	±1.51±0.10	±2.49±0.18	±2.45±0.16	±3.98±0.30	±2.45±0.16

Standard deviations of the three series of heterozygotes and of the bar and ultra-bar females.

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low facet number. Selection tends to eliminate germinal diversities which may be present in the stock before selection. Consequently in the bar stock the bar gene has a more uniform internal environment and one would expect that such a genotypic complex, when subjected to a uniform environment would give a less variable result than stocks in which the original germinal diversity were still present, such as ultra-bar and the heterozygotes.

The data strongly suggest that at the higher temperatures 29° and 31° that variability is increased. This is especially seen in the heterozygotes of the bar x ultra-bar, and bar x full crosses. This agrees with Vernon's statement that variability increases under unfavorable conditions. It is well known that at these temperatures the viability of Drosophia is reduced.

These results are in general agreement with those of Krafka (1920) where he states that the coefficient of variability increases with increase of temperature.

IV. The Effect of Temperature Upon Vital Processes In General.

Discussion and Conclusions.

It is an old observation that vital processes are affected by changes in temperature. The expression of this change has gradually become more exact and the physiological processes have been studied in greater and greater diversity. These processes include such diverse activities as respiration in plants, rate of segmentation, rate of growth, rate of regeneration, rate of heart beat, rate of nerve impulse, rate of pulsation of the contractile vacuole, and rate of motor activity. The great wealth of research on this subject has been summarized and extended by Kanitz (1915) and Matisse (1919) in their respective works, which give a systematic and critical account of our knowledge of the subject.

It has been found that for numerous vital processes Vant Hoff's rule (RGT rule) holds in much the same manner as it does for chemical reactions.

$$Q_{10} = \frac{V_{t+10}}{V_t} = 2 \text{ to } 3$$

Q_{10} is larger at the lower temperatures and smaller at the higher temperatures.

A more exact method for showing the rate of acceleration of a reaction with temperature is given by the formula of Arrhenius.

$$K_1 = K_0 e^{\frac{\mu}{2} \frac{T_1 - T_0}{T_0 T_1}}$$

For a great many chemical reactions the value of μ is between 12,000 to 16,000 and it has been shown by Arrhenius (1915 p. 55) that a number of physiological processes for which μ has been calculated gives this value. The constant of Arrhenius' formula is a more exact expression for the effect of temperature than Q_{10} of the RGT rule.

The empirical nature of these formulae must be remembered, however, and it is probably too sweeping a generalization to make that because a physiological process gives a value of Q_{10} or for μ similar to that of a chemical reaction that therefore the process is a chemical one. Physiological processes are tremendously complex, and it is certain that many chemical reactions and many physical processes interlock to give the result which constitutes the physiological action. Barry (1914) points out that the more complex a phenomenon is, the greater is the chance, on the theory of probability that it will follow Vant Hoff's rule. Bayliss also urges caution in the use of Vant Hoff's rule. Snyder has shown (1908) that the Q_{10} for muscle contraction gives a result which would suggest that it is a chemical reaction. Muscle contraction, however, has been shown to consist of three

phases, latent, shortening, and relaxation phases. The temperature coefficients for each of these three phases would indicate for instance that a physical process is involved in the latent period of contraction of cross-striated muscle. This example indicates the value of a study of Q_{10} for analyzing a particular process as well as to indicate the error which may result by concluding that because a process follows the RGT rule that, therefore, it is a chemical process.

Osterhout (1917) has indicated how in the organism, where chemical reactions of many sorts undoubtedly do go on, that one reaction may have to await the products of an earlier reaction, so that they all would be reduced to the uniform speed of diffusion. A word may be said here about other physical processes which go on in the cell beside diffusion, such as adsorption, absorption, surface tension, and those which result from the electrical charges on the immense internal surfaces of the cell. The work of R. S. Lillie (1922) suggests that electro-chemical processes play an important part in the organism. Crile (1922) says that the organism in its relation to temperature is similar to an electro-chemical cell.

In any case many processes of the organism are undoubtedly exponential functions of the temperature. And in accordance with the most general form of expressing such a relation the rate of decrease of facet count is expressed as the percentage decrease per degree.

As was pointed out above it is one more instance of a phenomenon which comes under the point of view of "the compound

interest law", along with such diverse processes as the law of cooling bodies, disintegration of radioactive substances, variation of atmospheric pressure with altitude, the absorption of actinic energy from light passing through an absorbing medium, and the relation between chemical reaction and temperature (Mellor, (1919) pages 56-66).

Although so many processes which go on in the organism obey this law in their relation to temperature, it does not follow that all processes follow this law. Krogh (1914) finds that for the embryonic development of certain amphibia, fish, insects, and echinoderms the relation between velocity and temperature cannot be expressed by Vant Hoff's formula, but that within rather narrow limits, the relation is a linear one. "The increment in velocity is proportional to the temperature increment." His formula is as follows:

$$K_{10} = V_{t+10} - V_t$$

Krogh (1914) finds further that the evolution of carbon dioxide by chrysalides of Tenebrio molitor also follows a linear law. These results disagree with those of Loeb and Wasteneys (1912), Lillie and Knowlton (1897) and Hertwig's data on the influence of temperature upon the development of frogs as calculated by Cohen. Following the method of Krogh, Krafka (1920) has obtained a straight line for the rate of development of Drosophila between 15° and 29° C.

There are some undoubted exceptions to the compound

interest law among vital processes. In addition to those which give a linear relation, there are some which show rather great changes within the limits of a few degrees. Processes of this sort were pointed out above, and strongly suggest viscosity changes. Ostwald and Fisher (1917, p. 85) speaking of the effect of temperature upon viscosity changes in gels say, "Within a temperature range of but a few degrees, there occurs a fall in viscosity from the values characteristic of solids to those characteristic of liquids." May these phenomena be explained by viscosity changes within the protoplasmic colloids? It is well known that the protoplasm of the cell oscillates between the more liquid and the more solid condition, and recent work especially that of Heilbrunn on viscosity changes during mitosis and the microdissection work of Chambers leave no doubt that great viscosity changes do occur and "must play an important part in the mechanics of many vital processes."

This is of further interest in view of the results that Laughlin (1919) has obtained in his study of mitosis and the temperature coefficients which the different phases show. For his stage # 6, an early anaphase, he finds that a rise in temperature decreased the speed of this particular stage, indicating that a physical process is probably involved. May this not be related to the result of Heilbrunn's that immediately before the division of the cell there is an increase in viscosity? In any case the fact is clear that protoplasmic activity is affected by temperature changes, and that many processes interlace to give the result which we call a physiological action,

and in an attempt to analyze these activities by means of temperature coefficients, it is uncertain what the exact nature of the process may be. It may be the resultant of many different processes, or it may be some more restricted process. In most cases the activity follows the exponential law, and the rate of change of facet decrease in homozygous and heterozygous flies over the range of temperatures from 15° to 31° C follows this rule. Dominance gives quite a different result in its temperature relation. Since dominance is a measure of a relation between two genes, we are taking a measure in a study of its temperature relations of something that occurs within rather narrow limits, and in a colloidal medium. To find what its real nature is depends upon future research.

IV. Summary.

1. An examination of the optic discs during the facet reaction period (which takes place between the time when 32% and 45% of development is completed) shows that temperature acts upon cells of an embryonic type, and not upon cells which show any structural differentiation that might suggest ommatidia.

2. Flies heterozygous for genes of the bar series of multiple allelomorphs are intermediate in facet count between flies homozygous for the same genes for the temperature range 15° C to 31° C.

3. Facet counts of flies heterozygous for genes of the bar series show an exponential decrease with increase in temperature. In this respect they resemble homozygous flies.

4. The temperature coefficients of facet decrease in heterozygotes is like that of homozygotes of one of the parental stocks, and is not intermediate.

5. Where ultra-bar is involved it is the more dominant gene. Bar is the more dominant gene in the full by bar cross.

6. Near 27° is a critical temperature for change in dominance, as it is for some other physiological processes. The dominance coefficient of the more dominant gene increases in both directions from this critical point.

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